Current Biology, Vol. 15, 1740–1744, October 11, 2005, ©2005 Elsevier Ltd All rights reserved. DOI 10.1016/j.cub.2005.08.045

The Interaction between Binocular Rivalry and Negative Afterimages

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Summary

Afterimage formation, historically attributed to retinal mechanisms [1–4], may also involve postretinal process [5–7]. Consistent with this notion are results from experiments, reported here, investigating the interaction between binocular rivalry and negative afterimages (AIs). In Experiment 1, one eye was exposed to a grating never consciously experienced by the observer because this grating remained suppressed in rivalry throughout induction (the exclusively dominant stimulus was designed to preclude formation of an AI). As expected, the suppressed grating generated a vivid AI whose orientation could be accurately identified; not surprisingly, the strength of this AI varied with induction contrast. Experiment 2 revealed, however, that the strength of this AI produced during suppression was significantly weaker than the AI produced by that same stimulus when it was visible throughout the entire induction period, implying that some component of AI induction is susceptible to interocular suppression. In Experiment 3, AIs of dichoptic, orthogonally oriented gratings were induced in a way ensuring that one of the two gratings was exclusively dominant during the induction period. Dissimilar monocular AIs engaged in rivalry, as expected, but, surprisingly, the AI induced by the suppressed grating initially dominated. We offer two alternative accounts of this counterintuitive finding, both based on differential neural adaptation.

Results and Discussion

The impetus for this study emerged serendipitously while we were investigating whether observers could detect the physical removal of patterns phenomenally suppressed from consciousness. In that study, a small sinusoidal grating was rendered invisible to visual awareness via binocular rivalry suppression, and at some point during this suppression period, the grating was physically removed. Interestingly, this removal could be reliably reported because observers typically perceived a negative AI after the removal of the suppressed pattern, with this AI often disrupting exclusive dominance of the "real" image presented to the other eye. Intrigued by these anecdotal observations, we investigated interactions between binocular rivalry and negative AIs in greater detail.

Our first experiment simply confirmed, with an objective technique, that AIs could be generated during suppression phases of binocular rivalry. Observers performed a two-alternative, forced-choice orientation-identification task following adaptation to a static grating (tilted ± 45° from vertical) during rivalry suppression (Figure 1A). Critically, observers never consciously perceived the static grating during AI induction. On each trial, they initially experienced binocular rivalry between a "pinwheel" and a vertically oriented grating—both of these rival patterns reversed in contrast every 200 ms to preclude formation of afterimages (confirmed by control experiments). The static, AI-inducing grating was presented only when observers declared the pinwheel exclusively dominant. Thus, performance on this task relied solely on the visibility of an AI induced by a grating that was never consciously perceived. Insofar as the neural adaptation involved in AI formation includes a retinal component [1–4], rivalry suppression—which itself arises from postretinal neural processes—should not abolish the formation of a negative AI.

As expected, suppressed gratings generated vivid AIs whose orientations could be identified accurately, as long as the inducing contrast was not too low (Figure 1B). The improvement seen in orientation identification when inducing contrast is increased is consistent with the functional relationship between afterimage strength and inducing contrast [8, 9]. Confirmation that AIs can be induced during suppression sets the stage for the following experiments.

Although it does not preclude formation of a negative AI, does suppression of an inducing pattern nonetheless influence the strength of the resulting AI? Published results provide seemingly conflicting answers to this question [7, 10]. To examine this question for ourselves, we compared the durations of AIs induced by gratings rendered invisible by rivalry suppression to those visible throughout the induction period (Figure 2A). This measure of AI strength, i.e., duration, correlates well with other estimates of AI strength [8, 9, 11], and in ancillary experiments, we confirmed that comparable results are also obtained with two other valid techniques, one based on nulling an AI and the other based on paired comparison of dichoptic AIs generated simultaneously, one by a suppressed inducer and one by a visible inducer (see the Supplemental Data available with this article online).

In fact, AIs induced during rivalry suppression were significantly weaker than AIs produced by the same stimulus when it remained visible throughout the entire induction period, a finding that dovetails nicely with results by Tsuchiya and Koch [7] published after completion of our study. The magnitude of this reduction in AI strength for two inducing contrasts is shown in Figure 2B, and readers can use the demonstration included in the Supplemental Data to experience this perceptual weakening by suppression.

Can we safely assume that the difference in AI strength between "visible" and "invisible" conditions is attributable to suppression during the induction phase and not some other, associated factor? There is good evidence that the dominance state during rivalry is

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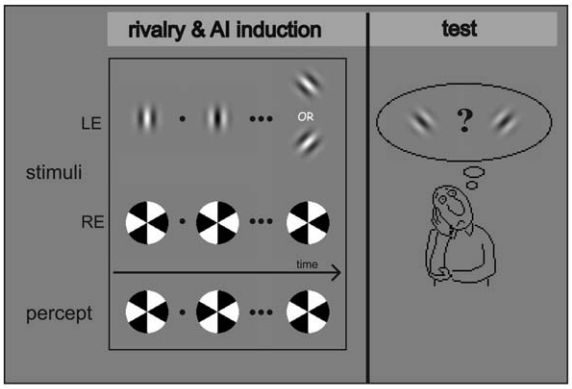

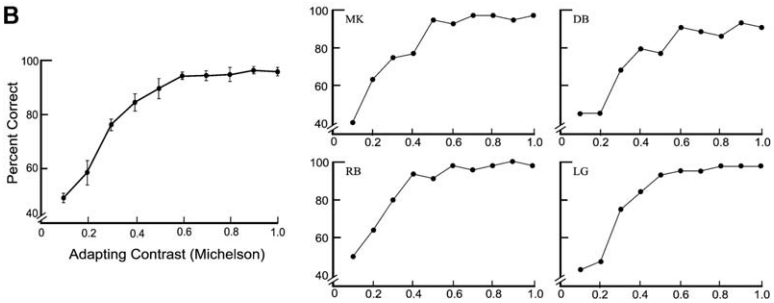

Figure 1. Experiment 1: Negative Afterimages of Suppressed Patterns

(A) Graphical depiction of a typical stimulus sequence. A pinwheel and a vertically oriented Gabor are independently presented to each eye, and binocular rivalry ensues. When observers declare the pinwheel exclusively dominant, the suppressed eye's stimulus changes to a static Gabor tilted 45° left or right of vertical. After 4 s of adaptation, both patterns are extinguished, and observers indicate the orientation of the resulting afterimage.

(B) Proportion of trials in which orientation was correctly identified as a function of inducing contrast (averaged across adapting eye). Error bars indicate ± 1 standard error of the mean (SEM).

equivalent to monocular, nonrivalry viewing [12], so it is reasonable to assume that our strategy for estimating the strength of a dominant AI is justified. Also, the radial grating alone does not generate an AI that, if it did, could have interfered with visibility of the grating AI at the time of test. Moreover, Tsuchiya and Koch [7] showed that a dynamic pattern producing rivalry suppression must be presented *simultaneously* with the dichoptic inducing grating in order to weaken an AI, implying that suppression is key to AI weakening. Finally, our results cannot be attributed to varying levels of attention during the induction periods. Indeed, it has been shown that attending to a figure during an induction phase actually weakens the subsequently experienced negative AI of that figure [6]. On the reasonable assumption that, in our Experiment 2, observers naturally attend to a visible, dominant inducer but not to an invisible, suppressed one, our results may actually provide a conservative estimate of suppression's weakening effect on AI formation. For all these reasons, we are confident that the reduction in AI strength is caused by suppression of the inducing pattern and not by some other, unspecified interaction between the two dichoptic stimuli.

Suppression's influence on AI strength implies that at least some component of AI formation resides at or beyond the neural site of dichoptic inhibition involved in rivalry. It is widely believed that the neural events underlying rivalry transpire within cortical brain areas [13], although the lateral geniculate nucleus (LGN), a subcortical, thalamic structure, could also play a role in rivalry in that the LGN has neurophysiological machinery for implementing dichoptic interactions [14–16]. In any event, our results, together with others' [5, 7], clearly demonstrate that AI formation is not strictly a retinal process.

In a final experiment, we turned our attention to another aspect of our initial anecdotal observations, the one suggesting that an AI could dominate a seemingly stronger, real image. In this last experiment, we simultaneously induced dichoptic, negative AIs to visible and invisible gratings during rivalry, and we examined rivalry between those AIs. Earlier work has shown that dissimilar monocular AIs engage in rivalry with dynamics similar to that produced when one views dissimilar monocular ("real") images [17, 18]. Experiment 2 revealed that AIs of visible patterns are stronger than AIs of suppressed patterns. Moreover, we know that dominance in rivalry favors the stronger of two rival patterns [19]. Putting these observations together, then, one would expect that an AI induced by a dominant grating should prevail over an AI induced by a suppressed grating because the former is stronger than the latter.

Dichoptic, orthogonally oriented AIs were generated during a single dominance/suppression phase of rivalry (Figure 3A). Flash suppression [20] and unequal grating contrasts ensured that one of the two gratings was exclusively dominant during the induction period. After 4 s AI induction, both patterns were extinguished, and observers reported the orientation of the initially dominant AI.

Contrary to expectation, the AI induced by the sup-

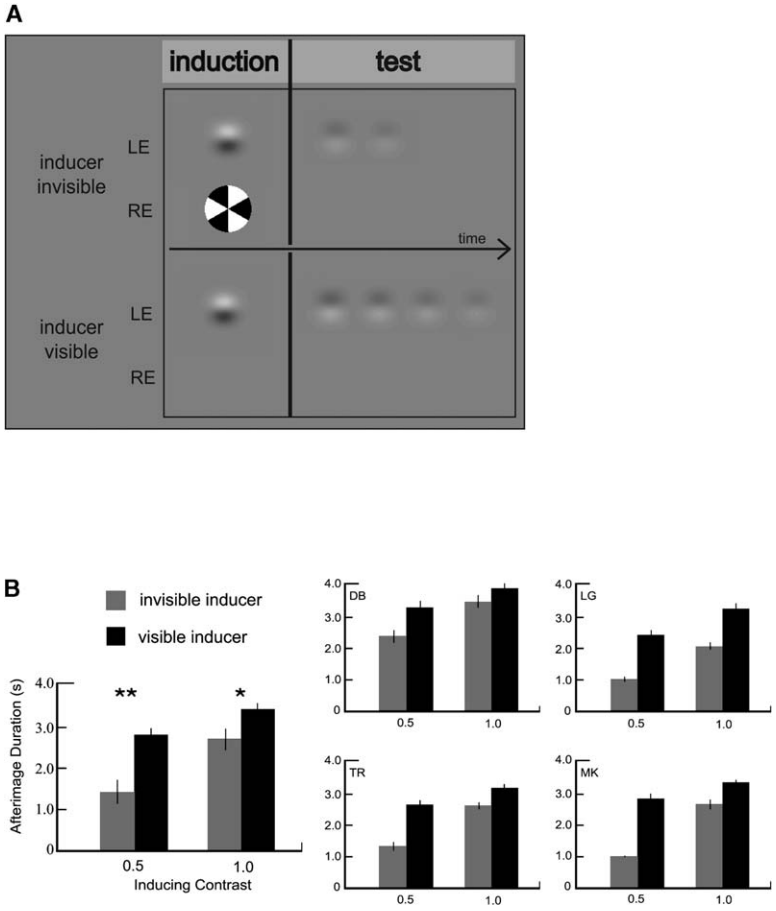

Figure 2. Experiment 2: Rivalry Suppression Weakens Afterimage Strength

(A) Graphical depictions of "invisible" and "visible" stimulus sequences. Observers initially experience binocular rivalry between a pinwheel and a vertically oriented Gabor (not shown). When observers declare the pinwheel exclusively dominant, the suppressed eye's stimulus changes to a static, low-spatial-frequency, horizontally oriented Gabor. For invisible trials, the pinwheel remains dominant, and observers never perceive the AI-inducing grating. For visible trials, the pinwheel is removed, and observers consciously perceive the inducing grating. After 4 s of adaptation, both patterns are extinguished, and observers indicate the duration of the resulting afterimage.

(B) Average durations (in seconds) of afterimages to gratings rendered invisible by rivalry suppression (gray bars) and those visible throughout induction (black bars). For both levels of inducing contrast, the difference in afterimage duration for visible and invisible inducers was statistically significant (** $t_3 = 7.86$, $p < 0.01$; * $t_3 = 4.18$, $p < 0.02$). Error bars indicate ± 1 SEM.

pressed grating was *more* likely to dominate initially in rivalry (Figure 3B). This result seems counterintuitive considering that the AI induced by a suppressed pattern is weaker in strength. Moreover, one would also expect the dominant rival stimulus during the induction phase to remain dominant as an AI because observers were presumably attending to that pattern, which in other circumstances is known to promote initial dominance [21]. Why, then, does a weak negative AI produced by a suppressed inducer dominate in AI rivalry? The answer to this question depends, in part, on the neural events underlying the formation and the subsequent visibility of negative AIs, and as others have stressed, it is important to distinguish these two aspects of AI perception [6, 8, 11]. Perceptually, a negative AI appears as a polarity-inverted replica of the inducing pattern, implying that AI formation involves adaptation of neurons selective for the spatial distribution of lightness and darkness within their receptive fields. Such neurons, which are known to exist in the retina, LGN, and primary visual cortex, are typically characterized as phase sensitive. Conversely, phase-*in*sensitive neurons respond regardless of the spatial phase of the distribution of lightness and darkness—neurons of this type would be relatively uninvolved in AI formation. Both categories of neurons, however, could mediate AI visibility, and, hence, adaptation of both categories of neurons could contribute to the reduced visibility of an AI [8, 11]. With these ideas in mind, several possible explanations for the results of Experiment 3 can be reasonably entertained.

The tendency of an AI induced during suppression to dominate initially could reflect the involvement of adaptation in producing switches in dominance during binocular rivalry. Models of binocular rivalry posit that alternations between rival perceptual interpretations result from fluctuations in activity associated with the neural representations of the competing patterns. These fluctuations in neural activity arise, in part, as a result of self-adaptation that is proportional to current levels of activation—neural elements associated with the currently dominant pattern progressively adapt to a greater extent than those associated with the suppressed pattern [22, 23], eventually culminating in a perceptual switch. Perhaps, then, adaptation of phase-sensitive mechanisms during AI induction engages neural mechanisms that mediate perceptual alternations in binocular rivalry. Differential adaptation during rivalry reduces sensitivity to the dominant pattern more than the suppressed pattern, and, as a result, the AI of the suppressed grating initially wins the competition for awareness.

By this account, the initial bias to perceive the AI induced by the suppressed grating should depend critically on the duration of the induction period. For longer induction periods, we assume that continuous, differential adaptation eventually promotes a perceptual switch—the suppressed grating becomes dominant in

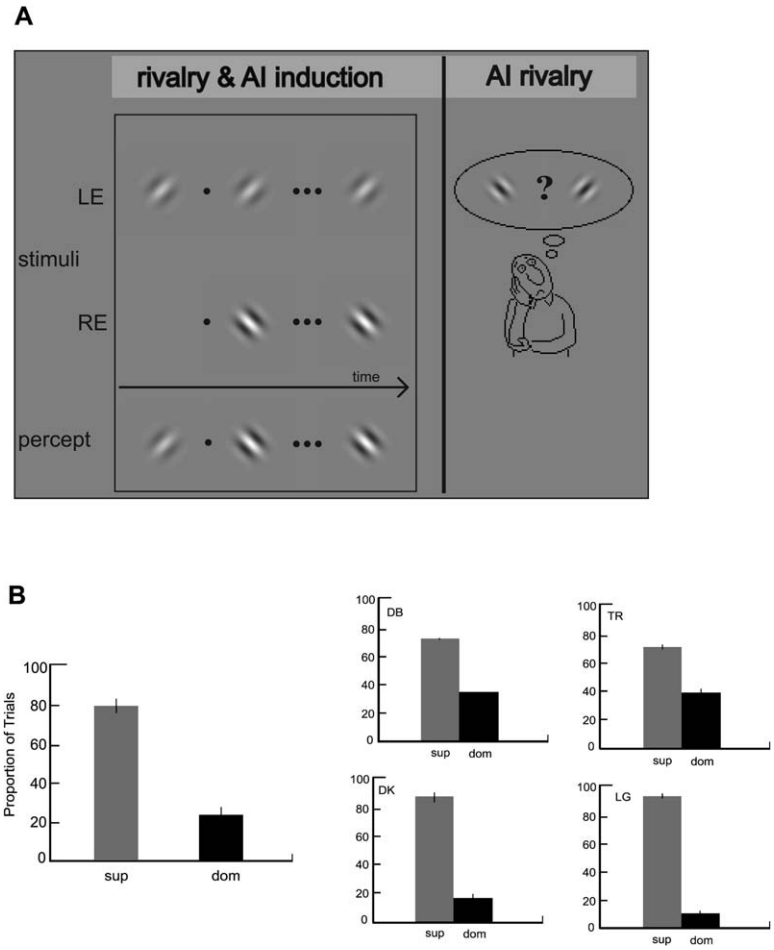

Figure 3. Experiment 3: Rivalry between Afterimages Induced During Rivalry

(A) Simultaneous, orthogonal afterimages are induced during a single phase of binocular rivalry. After 4 s of adaptation, both patterns are extinguished, and observers indicate the orientation of the initially dominant afterimage.

(B) Proportion of trials in which the afterimage of the suppressed grating (gray bars) and the afterimage of the dominant grating (black bars) initially dominated rivalry. Error bars indicate ± 1 SEM.

awareness, and the previously dominant grating becomes suppressed. For shorter induction periods, however, differential adaptation would be less pronounced, and, therefore, the tendency to perceive the AI of the suppressed grating should be reduced. This prediction was confirmed by an ancillary experiment in which the induction period was reduced to 2 s. For one observer, the bias to initially perceive the AI of the suppressed grating remained, but was greatly reduced. For two other observers, the bias reversed; they tended to initially perceive the AI of the dominant grating (see Supplemental Data).

So, selective adaptation of phase-sensitive neurons, implied by the generation of negative AIs, also could be involved in promoting alternations in dominance during rivalry. This, in turn, could link binocular rivalry with another aspect of binocular vision, one thought to involve activity within phase-sensitive neurons: the registration of binocular retinal disparity [24].

There is, however, an alternative account of the present results that deserves consideration, an account portraying the notion of "AI strength" in rather different terms. Perhaps a "strong" AI (operationally defined in terms of AI duration or in terms of perceived contrast) results from a relatively weak response within those phase-sensitive neural elements affected during induction, with that weak response resulting from strong adaptation during the induction period. Suppression of a stimulus during the induction phase would diminish the strength of adaptation, thereby producing an AI that was weaker in appearance yet, by the same token, one that was stronger in terms of its residual neural responsiveness and one, therefore, more likely to contribute to initial dominance during AI rivalry. This account parsimoniously explains the results from Experiments 2 and 3 within a single framework that combines rivalry suppression and afterimage formation.

The present results do not allow us to distinguish between these two hypotheses, and in the final analysis, that distinction will depend upon knowing more about the neural bases of AI formation and visibility. Still, we can conclude with confidence that binocular rivalry suppression, as well as the allied form of interocular suppression studied by Tsuchiya and Koch [7], significantly affects neural events underlying AI formation. This conclusion confirms that AI formation is not solely a retinal process and, moreover, implies that the neural footprints of rivalry suppression can be traced to relatively early stages of visual processing.

Experimental Procedures

Experiment 1

Rival stimuli consisted of a vertically-oriented Gabor patch and a pinwheel. The spatial frequency and standard deviation of the Gabor patch were 3.0 cyc/deg and 0.26°, respectively. The diameter of the pinwheel was 1.58° and was composed of six alternately

light (63.43 cd/m^2) and dark sectors (<0.01 cd/m^2). The static, afterimage (AI)-inducing grating was a Gabor patch of the same dimensions but tilted ± 45° from vertical. In separate trials, its Michelson contrast varied from 0.1 to 1.0 in steps of 0.1 about a mean luminance of 31.39 cd/m^2. Surrounding each rival pattern were two black-and-white frames, which promoted stable fusion during dichoptic viewing. All stimuli were presented in the center of a gamma-corrected Mitsubishi Diamond Pro 2020u monitor (1024 × 768; 120 Hz) with the screen luminance set to the mean luminance of the Gabor patches. Observers viewed the display through a mirror stereoscope from 82.55 cm (maintained by a chin rest).

At the start of each trial, the Gabor patch and pinwheel reversed contrast at 5 Hz to prevent the formation of negative AIs. Participants tracked rivalry between the two patterns until they indicated, via keypress, that the pinwheel was exclusively dominant. Following a 500 ms delay, the counterphase horizontal Gabor was extinguished, and the static AI-inducing Gabor gradually faded in over 1 s. Observers adapted to the static Gabor for 4 s, as long as they continued to perceive the pinwheel as the dominant stimulus (failure to maintain dominance of the pinwheel for the entire induction period resulted in the termination of adaptation, and the trial was retested). After induction, both eyes' stimuli were replaced with homogeneous fields at mean luminance (fusion frames remained on the screen), and participants indicated the orientation of the AI by pressing one of two predesignated keys. After each trial, counterphase pinwheels were presented to both eyes for 2 s to extinguish any residual AIs (confirmed with control experiments).

Participants were the two authors and three experienced psychophysical observers naïve to the purpose of the experiment. Because each trial was contingent on individual observers' percepts, the duration of each trial varied both within and among observers. The orthogonal combination of ten inducing contrast values and two spatial configurations (the adapting Gabor was presented to the right and left eyes equally often) resulted in 20 distinctive trials, each of which was repeated three times in blocks of 60 trials. Each participant completed eight blocks of trials.

Experiment 2

The stimuli, apparatus, and procedures were the same as in Experiment 1, except for the following changes. For half of the trials, the AI-inducing grating was suppressed from awareness during binocular rivalry. For the remaining trials, the rival pinwheel stimulus was not presented, and the AI inducing grating was visible throughout the induction period. The AI-inducing Gabor was oriented, horizontally and its spatial frequency was reduced to 1.0 cyc/deg, stimulus conditions that should minimize any residual neural blurring effect produced by small, involuntary, horizontal eye movements. After 4 s of adaptation, observers indicated AI duration by holding down a predesignated key as long as the AI was visible.

Participants, the two authors and two observers naïve to the purposes of the experiment, each completed six blocks of trials. The orthogonal combination of two conditions, two inducing contrast values, and two spatial configurations resulted in eight distinctive trials, each of which was repeated four times within blocks of 32 trials.

Experiment 3

The stimuli, apparatus, and procedures were the same as in Experiment 1, except that simultaneous AIs were generated to Gabor patches oriented ± 45° from vertical. The Michelson contrasts of the dominant and suppressed inducing gratings always were 1.0 and 0.5, respectively. Each trial began with the presentation of the low-contrast grating to one eye, followed 500 ms later with the presentation of the high-contrast grating to the other eye (flash suppression). After 4 s of exclusive dominance of the high-contrast Gabor, both patterns were extinguished, and observers reported the orientation of the initially dominant AI.

Participants, an author and three observers naïve to the purpose of the experiment, completed three blocks of trials. The orthogonal combination of two grating orientations and two spatial configurations resulted in four distinctive trials, each of which was repeated four times within blocks of 16 trials.

Supplemental Data

Supplemental Data include Supplemental Experimental Procedures and two supplemental figures and are available with this article online at: http://www.current-biology.com/cgi/content/full/15/19/1740/DC1/.

Acknowledgments

This work was supported by National Institutes of Health grants EY13358 and T32EY07135. We thank two anonymous reviewers for helpful comments on an earlier version of this manuscript.

Received: July 7, 2005
Revised: August 2, 2005
Accepted: August 11, 2005
Published: October 11, 2005

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